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ASAS CENTENNIAL PAPER: Net energy systems for beef cattle— Concepts, application, and future models¹

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ABSTRACT: Development of nutritional energetics can be traced to the 1400s. Lavoisier established relationships among O₂ use, CO₂ production and heat production in the late 1700s, and the laws of thermodynamics and law of Hess were discovered during the 1840s. Those discoveries established the fundamental bases for nutritional energetics and enabled the fundamental entity ME = retained energy + heat energy to be established. Objectives became: 1) to establish relationships between gas exchange and heat energy, 2) to devise bases for evaluation of foods that could be related to energy expenditures, and 3) to establish causes of energy expenditures. From these endeavors, the basic concepts of energy partitioning by animals were developed, ultimately resulting in the development of feeding systems based on NE concepts. The California Net Energy System, developed for finishing beef cattle, was the first to be based on retained energy as determined by comparative slaughter and the first to use 2 NE values (NE_m and NE_g) to describe feed and animal requirements. The system has been broadened conceptually to encompass life cycle energy requirements of beef cattle and modified by the inclusion of numerous adjustments to address factors known to affect energy requirements and value of feed to meet those needs.

The current NE system remains useful but is empirical and static in nature and thus fails to capture the dynamics of energy utilization by diverse animals as they respond to changing environmental conditions. Consequently, efforts were initiated to develop dynamic simulation models that captured the underlying biology and thus were sensitive to variable genetic and environmental conditions. Development of a series of models has been described to show examples of the conceptual evolution of dynamic, mechanistic models and their applications. Generally with each new system, advances in prediction accuracy came about by adding new terms to conceptually validated models. However, complexity of input requirements often limits general use of these larger models. Expert systems may be utilized to provide many of the additional inputs needed for application of the more complex models. Additional information available from these systems is expected to result in an ever-increasing range of application. These systems are expected to have increased generality and the capability to be integrated with other models to allow economic evaluation. This will eventually allow users to compute solutions that allow development of optimal production strategies.

Key words: beef cattle, feeding system, net energy

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INTRODUCTION

Knowledge of nutritional energetics has followed a recognizable pattern of evolution from novel fundamental insights leading to development of creative concepts, integration to create applicable principles, and application of those principles to explain life process-

es. Subsequently, during the adoptive-dissemination phase, those principles are applied to yield solutions to industry or societal problems. Nutritional energetics has been largely in the adoptive-dissemination phase for approximately 100 yr. For example, methods to chemically analyze feed and NE concepts were developed. Those methods and concepts were used for the development of NE-based feeding systems. The purpose of this review is to describe the discovery of concepts underlying nutritional energetics and application of those principles to the development of feeding systems for beef cattle. This review describes some of the limitations of the current systems and briefly provides examples of how mathematical modeling has been ap-

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plied to better capture known biological principles as related to nutritional energetics. In addition, we have attempted to offer a vision of how currently available knowledge and technology may be applied to enable development of strategies for optimizing beef cattle production systems. This is a review of the literature and as such provides a historical overview of the field of nutritional energetics. Readers are strongly encouraged to visit original works should detailed descriptions be needed.

Historical

The historical development of nutritional energetics was reviewed by Brody (1945), Kleiber (1961), and Blaxter (1962). Many aspects of animal energetics have been reviewed by Garrett and Johnson (1983), Baldwin (1995), and Johnson et al. (2003). We have relied on those treatises heavily for this synopsis. Utilization of dietary energy has been a subject of research since the eras of Leonardo da Vinci (1452 to 1519), Joseph Priestly (1733 to 1804), and Antoine-Laurent Lavoisier (1743 to 1794). From these and other philosophers and researchers, the generalization was developed that life is primarily a controlled combustion process. In 1780, Lavoisier and Laplace reported their breakthrough observations establishing the relationship between O₂ use, CO₂ production, and heat production. This breakthrough concept that related metabolism and combustion permitted the formulation of the following equation:



It should be recognized that evolution of this concept from da Vinci's observations that animals could not survive in an atmosphere that would not support a flame to those proposed by Lavoisier and eventually accepted required well over 300 yr. It is also noted that the development and acceptance of the theory of combustion and metabolism was severely delayed by the general acceptance of the phlogiston dogma (which stated that objects burn because they lose a combustible substance called phlogiston instead of actually gaining something, O₂, as was later shown).

After those pioneering works, new objectives of research in nutritional energetics became to 1) establish relationships between gas exchange and heat production, 2) devise bases for evaluation of foods that could be related to energy requirements and energy expenditures, and 3) establish causes of energy expenditures. The laws of thermodynamics that are fundamental to nutritional energetics were developed in the 1840s. The first law of thermodynamics holds that energy can neither be created nor destroyed but can be transformed from one form to another. This law is essential to measurements and calculations used in nutrition. It, for example, dictates acceptance of the equality:

$$\text{ME} = \text{RE} + \text{HE},$$

where ME = the energy consumed by an animal that is not excreted in feces, urine, or combustible gasses; RE = retained energy, energy deposited in animal tissues or products; and HE = heat energy, heat generated by the animal. Thus, if 2 of these entities are measured, the third can be calculated by difference. The second law of thermodynamics states that all forms of energy can be quantitatively converted to heat. This law and the law of Hess, which states that heat lost in a chemical reaction is independent of path, are the basis for all measurements made in nutritional energetics. These laws dictate that, for example, if one measures the heat released from total oxidation of 1 g of carbohydrate to CO₂ and H₂O in a laboratory bomb calorimeter, the result will be the same as the heat released when 1 g of that carbohydrate is totally oxidized by an animal.

The adiabatic bomb calorimeter was developed by Berthelot (1827 to 1907), which enabled reproducible and accurate determination of the GE contents of organic compounds, feed, feces, and urine. Another essential advance was the development of the concept that foods should be partitioned into carbohydrates, fats, and proteins, because their metabolism differed. Primary contributors to this concept were Baron Justus Von Liebig (1803 to 1873) and his students. Liebig maintained that a considerable part of animal food, especially minerals and proteins, does not function as fuel but as material for body building. In 1881, Lunin concluded that animals need some unknown substance, other than carbohydrates, fat, minerals, and protein. Those substances were later called vitamins by Funk (1912).

Considerable effort, over a period of 100 yr or so, was devoted to establishing relationships between gas exchange and heat production. One of Liebig's students, Carl Von Voit, utilized the open-circuit respiration apparatus of Max Von Pettenkofer (1818 to 1901), the prototype of modern instruments, to do extensive energy balance experiments. Instrumentation of this type was utilized extensively by the groups of Henry Armsby, Wilbur Atwater, Oskar Kellner, and Max Rubner (all students of Von Voit). Recently, more mechanically or electronically sophisticated instruments, or both, based on similar principles, have been in use at Beltsville Agricultural Research Center (Flatt et al., 1965), Colorado State University (Johnson, 1986), and the US Meat Animal Research Center (Nienaber and Maddy, 1985). Some of the early instrumentation, such as that of Regnault (1810 to 1878), was of the closed-circuit type. Closed-circuit systems were used extensively for man and smaller animals and some for larger animals (e.g., Hannah Institute; Wainman and Blaxter, 1958) but were never as widely used as the open-circuit type. It may be argued that work in this area, to a large degree, culminated in 1965 with the publication of the Brouwer equation (Brouwer, 1965). The equation was

developed to calculate heat production (H, kcal) from O_2 consumption (O_2 , L), CO_2 (CO_2 , L), and CH_4 production (CH_4 , L), and urinary N (N, g). The equation:

$$H = 3.866 \times O_2 + 1.200 \times CO_2 - 0.518 \\ \times CH_4 - 1.431 \times N$$

has been used almost exclusively for the calculation of heat production from indirect calorimetry measurements since its publication.

Direct calorimetry is the direct measurement of heat produced by the animal and is also founded in the work of Lavoisier. Atwater, Armsby, and Blaxter, among others, used instruments based on those principles. Although instrumentation has changed immensely, calorimeters in use at the University of Nebraska (Nielsen et al., 1997) were founded in those concepts.

In conjunction with establishing relationships between gas exchange and heat production and determining causes of animal energy expenditures, several groups devoted tremendous effort toward devising bases for evaluation of foods that could be related to energy requirements and energy expenditures. The starch equivalent system, developed by Oskar Kellner and his group (Kellner and Köhler, 1900; Kellner, 1909) was a net energy-based system in which the energy values of feedstuffs were expressed relative to that of starch to meet the energy needs of the animal for fattening. The starch equivalent system had a great influence in the practical feeding of livestock. It was used as the primary system throughout Europe and Russia for many years and served as the basis on which many others have been built. Atwater and associates (Atwater and Bryant, 1900) developed the physiological fuel values (PFV) system. Atwater's system was based on ME values of carbohydrates, fat, and protein, with the energy values of protein adjusted for the energy value of excreted urea. The PFV system remains the basis for expressing the energy (caloric) content of foods for human beings and laboratory animals. Armsby (1903, 1917), also used respiration calorimetry of the Atwater-Rosa type. He defined ME (PFV) as the NE plus heat increment of feeding. Armsby and his associates developed many of the principles on which current NE systems are based. Energy systems used in the United Kingdom (ARC, 1965, 1980; AFRC, 1990), France (INRA, 1978, 1989), and Australia (AAC, 1990) were grounded in principles derived from those earlier efforts.

The general equation $ME = RE + HE$ has been recognized since the days of Von Liebig, but, for many years, the primary effort of energetics researchers was to describe and quantify the ME of food and HE with RE, seemingly a secondary consideration. Lawes and Gilbert (1861) first employed the comparative slaughter method in experiments. Those experiments were of considerable interest, because they demonstrated for the first time that carbohydrates were the major source of energy leading to the synthesis of fat. Blaxter (1962)

stated that "during the last 100 yr, the complete bodies of about 250 cattle and 60 sheep have been analyzed" by the scheme that partitioned the animal into weight of gut contents, body water, body fat, body protein, and body minerals. Garrett et al. (1959) popularized the comparative slaughter technique in their classical manuscript, "The comparative energy requirement of sheep and cattle for maintenance and gain." This concept was further developed and refined then published as an article titled "A system for expressing net energy requirements and feed values for growing and finishing beef cattle" (Lofgreen and Garrett, 1968), which stands as the basis of the system incorporated into subsequent NRC (1976, 1984, 1996, 2000) recommendations. It should be noted that this system, like other systems currently in use, was rooted in the concepts developed by Armsby, Atwater, Kellner, Brody, Kleiber, Blaxter, and others; but unlike many of the systems, requirements and value of feedstuffs to meet those requirements were based on the measurement or estimation of energy retained, rather than energy losses.

Much of the essence of the last 50 yr of animal energetics research is captured in 16 publications from the symposia on energy metabolism of farm animals held every 3 yr beginning in 1958. Researchers Van Es (1994) and Flatt (2000) have summarized interesting portions of the history of the people and their work. Also of note is a report (NRC, 1935) of a conference sponsored by the Committee on Animal Nutrition of the National Academy of Science held at Pennsylvania State College in 1935 that features papers by Forbes, Mitchell, Brody, Klieber, and Ritzman.

Development of Feeding System Models

The basic definitions and concepts that underlie feeding systems currently in use were developed primarily by Armsby, Atwater, Kellner, and Rubner (all students of Von Voit), from application of indirect and direct calorimetry. Basic definitions (Figure 1) of GE, DE, ME, NE, NE_m , specific dynamic action, and work of digestion were established. The terms heat increment of maintenance and heat increment of production were adopted later to designate the energy costs of digestion and assimilation of food for maintenance and to indicate the energy costs associated with product formation, respectively. Numerous other terms have been invented and used to describe energy transactions in animals.

A subcommittee of the Committee on Animal Nutrition of the NRC (1981) developed terminology for an in-depth description of energy utilization that is consistent with most feeding systems currently in use. In this classical partition of dietary energy (Figure 1), energy consumed as food (intake energy) is lost as fecal energy, urinary energy, gaseous energy, or HE, or recovered as product. Heat energy can be further partitioned into that associated with basal metabolism, voluntary activity, product formation, digestion and absorption,

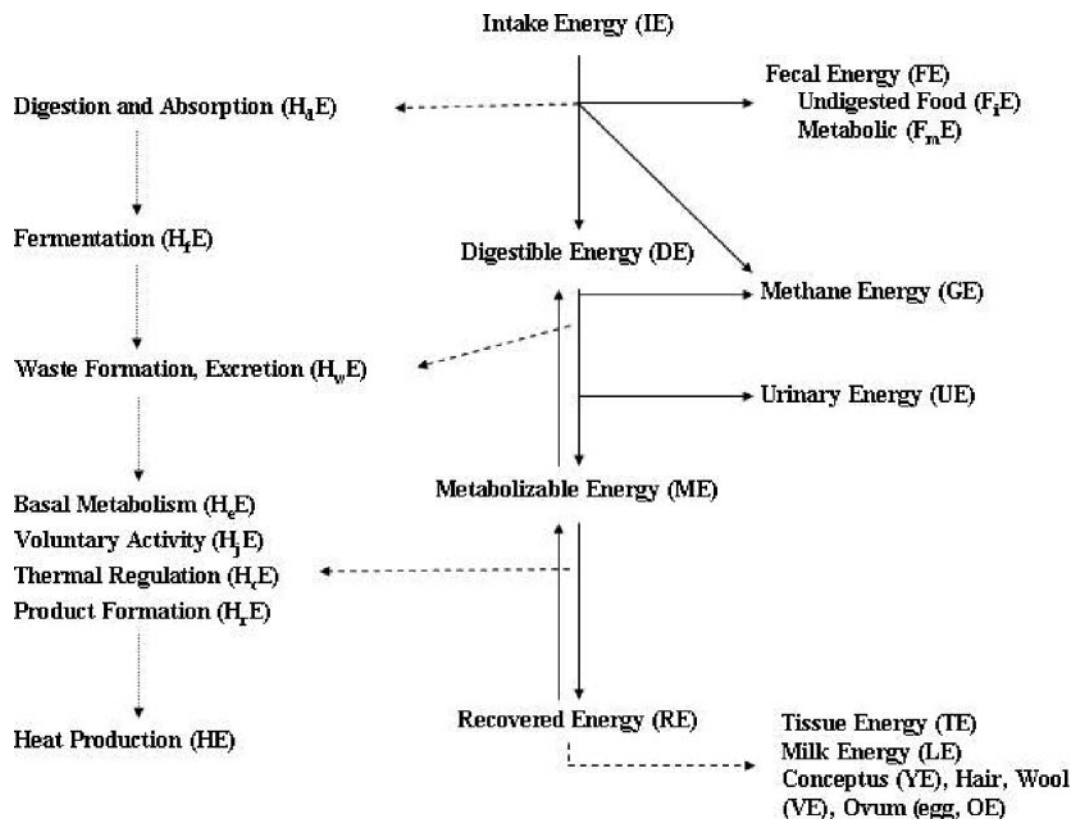


Figure 1. Schematic partition of energy in the animal (NRC, 1981).

thermal regulation, heat of fermentation, and waste formation and excretion. Partition of HE into meaningful physiological or metabolic components is the most difficult and controversial aspect of all systems. Net energy in product may be identified as body protein, body fat, conceptus, milk, hair, etc. It is notable that the largest energy losses are as fecal energy and heat and that RE constitutes a relatively small proportion (generally <20% in beef cattle) of intake energy (Figure 2).

A system for evaluating feeds should: 1) enable the value of feeds to be assessed as substitutes for one another, 2) permit determination of the quantity of feed to support a particular management goal, and 3) enable an estimate of animal performance if feed intake is known. Based on the widely held view that ME is a measure of the energy available for use by the body, several systems generally based on feed values and animal needs in terms of ME were developed. These included the PFV system developed by Atwater and associates (Atwater and Bryant, 1900), which remains in use for human and laboratory animals, and the total digestible nutrient (TDN) system. The NRC systems for poultry and swine are further examples of applications of these concepts. Other systems were developed to evaluate feeds based on their NE values for specific functions such as maintenance, growth, fattening, and lactation. The starch equivalent system of Kellner and associates (Kellner and Köhler, 1900), based on the

NE values of feeds for fattening, was the most widely adopted example of a system based on NE concepts. The ARC (1965, 1980) used ME as a beginning point, but by adjusting ME values for differing dietary quality and by applying estimates of efficiency of ME use for different physiological functions (i.e., maintenance, k_m ; growth; pregnancy, k_p ; lactation; etc.), the system was effectively a NE system. The NRC systems for beef (NRC, 1976, 1984) and dairy cattle (NRC, 1989) are additional examples of systems that are based on NE concepts and use NE values for maintenance, growth, pregnancy, and lactation.

The energy values of foods used in the PFV system are called PFV and are essentially ME values determined at maintenance rates of food intake. A correction for urinary N losses from dietary protein essentially adjusts protein intake to a carbohydrate energy equivalent and approximately reflects the energy cost of urea synthesis and the energy content of urea excreted into the urine. No correction is used for energy losses due to gaseous products of digestion, because these products are generally not of importance in nonruminants. Currently used tables of PFV reflect results from more recent digestibility studies in humans.

The energy values used for feeds in the TDN system were calculated from estimates of the digestible chemical components of feed as:

$$\text{TDN} = \text{DCP} + \text{DFIBER} + \text{DNFE} + \text{DEE} \times 2.25,$$

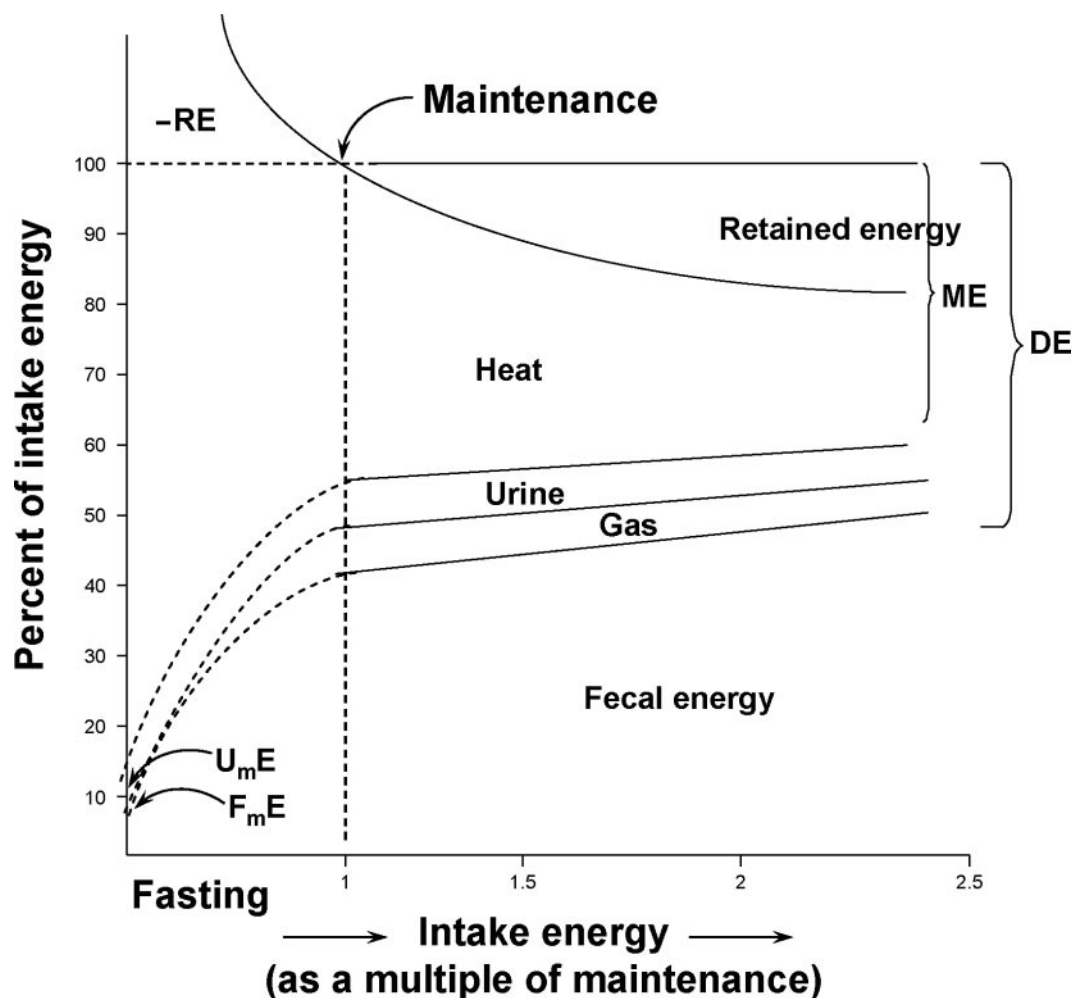


Figure 2. Schematic representation of the typical influence of intake level on the partition of intake energy for cattle consuming moderate-quality forage diets.

where TDN is expressed as pounds per pound or percentage and DCP, DFIBER, DNFE, and DEE = digestible crude protein, fiber, N-free extract, and ether extract, respectively. Animal requirements are estimated by summing tabular values of TDN required for maintenance, gain, milk, and activity.

In the starch equivalent system, feed values were measured as the amount of energy stored as fat per kilogram of feed provided above maintenance. Those determined values were expressed relative to the energy retained per kilogram of starch provided above maintenance. Animal requirements were estimated as the simple sum of requirements for maintenance, growth, and lactation.

Limitations of Early Systems

Several problems in the TDN system were recognized early. One was that maintenance was based on observations of Rubner that heat production at maintenance varied across species as a function of surface area which was estimated as $W^{0.67}$. Kleiber (1932, 1947) and Brody (1945) subsequently developed interspecies relationships between fasting heat production (FHP)

and BW, which led to the adoption of the allometric equation:

$$\text{FHP} = aW^{0.75}$$

where a was equal to 70 when the equation was applied to young adults across species (mice to elephants). It was recognized early that application of the concept of metabolic body size ($W^{0.75}$) within a species led to considerable variation in the coefficient (a). The coefficient differed due to age, previous plane of nutrition, physiological state, and sex and differed between species. It is generally agreed that no serious errors are incurred by the use of $W^{0.75}$ as a scaling factor in energy metabolism studies with ruminants when comparisons are necessary among or even within species. Most current systems accommodate variation in FHP and apparent maintenance requirements by adjusting the coefficient (a).

A major problem with the TDN system was that TDN values measured for forages and concentrates, when fed to ruminants, were not additive. Animal performance was less when TDN was from forage than when TDN was from concentrates. In addition, the relative

values of TDN from forages and concentrates were not constant but differed when used for different animal functions (e.g., maintenance, growth, milk). These problems are not easily corrected. Differences in true feeding value of forages and concentrates are partially due to greater CH_4 production during fermentation of forages. Additional contributors to the nonadditivity of forage and concentrate TDN are differences in heat losses during fermentation, differential changes in digestibility with altered intake, and differences in products of fermentation and their differing efficiencies of utilization within the animal. All of these tend to vary as functions of energy density of the diet and are generally reflected in diet digestibility or metabolizability. Thus, for example, the ARC (1980) system incorporated adjustments to diet ME based on level of intake and energy density of the diet.

The major problem encountered with the starch equivalent system, which was widely used in Europe, was similar to that of the TDN system. The relative energy values assigned to feeds were not additive across functions. In the starch equivalent system, feeds were evaluated solely on their efficiency of use for fat gain. However, relative values of feeds differ when used for functions other than fat gain. For example, dietary fat is substantially overvalued, but forage is undervalued relative to corn or starch when used for maintenance.

Development of NE Systems for Beef Cattle

It was long recognized, as indicated previously, that dietary ME is used with differing efficiencies depending on source, intake level, and function for which it is used by the animal. This created substantial problems with determining the nutritive value of feedstuffs and quantitatively expressing the results as a single value. As a result, ME has become the basic beginning point for the development of NE systems. To determine the partial efficiency of ME use or NE values requires more than one level of feeding. Because the relationship between ME intake (MEI) and energy balance is curvilinear over the entire range of feed intake, NE values are not constants but are influenced by the intakes over which the measurements are made (Garrett and Johnson, 1983).

The concept of using separate partial efficiencies (Figure 3) of ME utilization for maintenance and productive purposes (i.e., below and above maintenance) did not become established until the early 1960s. Blaxter (1961) in summarizing research on energy metabolism of sheep and cattle presented separate discussions for the utilization of dietary energy for maintenance and lipogenesis. Another paper (Blaxter and Wainman, 1961) defined the net availability of ME for production as the slope of a linear regression between positive energy retention and ME intake. The net availability of ME for maintenance was the slope of a linear regression between negative energy retention (energy loss) and ME intake. Interrelationships between metaboliz-

ability and partial efficiencies of ME utilization were further discussed in subsequent papers (Blaxter and Wainman, 1964; Blaxter et al., 1966). The curvilinear relationship between RE and MEI was approximated by 2 linear relationships, 1 above and 1 below maintenance, and the symbols for partial efficiencies were replaced by k_m and k_p . Blaxter and Graham (1955) and Blaxter (1962) partially outlined a feeding system, which, with modification, was developed into a feeding system on which much later work is based by a committee of the ARC (1965).

During the same time period, NE concepts as a means to establish more accurate feeding standards were investigated at the University of California, Davis. Rather than calorimetric methods employed by Blaxter and associates, comparative slaughter procedures were used with growing-finishing beef cattle and sheep. Those procedures were later reported by Lofgreen (1965). Results reported by Garrett et al. (1959) were the first of a series (Lofgreen, 1963a,b; Garrett et al., 1964) that led to a practical NE system for use by cattle feeders. The system was first introduced to the cattle industry in 1963 (Lofgreen, 1963a,b) and later revised and published (Lofgreen and Garrett, 1968). This system, subsequently known as the California Net Energy System (CNES), assigned 2 NE values to each feed – NE_m for maintenance and NE_g for energy gain. Animal requirements were stated using the same terms. The terms, NE_m and NE_g are related to k_m and k_p as follows:

$$\text{NE}_m = k_m \times \text{ME} \text{ and } \text{NE}_g = k_g \times \text{ME}.$$

The CNES was the forerunner of several systems developed that used NE as the basis for feeding standards. The CNES broke tradition and assigned 2 energy values to feedstuffs rather than the traditional single estimate. The CNES was basically an empirical system that was developed using data from long-term, comparative slaughter feeding trials (primarily using British and British crossbred steers and heifers) to determine the NE requirements for maintenance and growth of growing ruminants. Separation of requirements for maintenance and growth recognized different efficiencies of ME use for maintenance and growth. The CNES, originally proposed for growing beef cattle, was subsequently used as the basis for expressing energy requirements for maintenance and production of breeding cattle (NRC, 1976) and sheep (NRC, 1985). Requirements for lactation were listed in terms of NE_m because the efficiency of ME use for lactation changes with diet similar to changes in the efficiency of ME use for maintenance. Requirements for pregnancy were also expressed in NE_m equivalents based on efficiency of ME use for conceptus growth and maintenance of 13% (Rattray et al., 1974; Ferrell et al., 1976).

The ARC (1965, 1980) system and several other NE systems (INRA, 1978, 1989; NRC, 1989; AAC, 1990) were conceptually similar to the CNES but differed

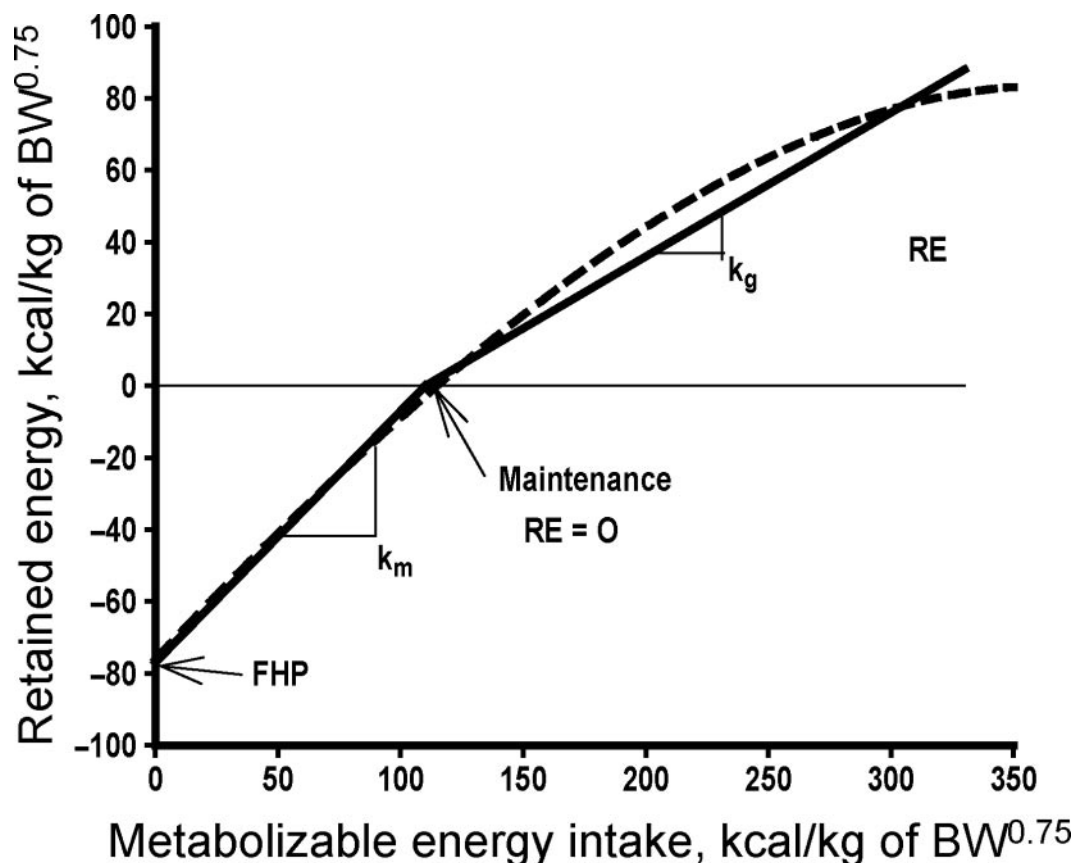


Figure 3. Representation of the relationship between retained energy (RE) and ME. The dashed line shows the curvilinearity between RE and ME and was derived from the relationship between log heat production and ME intake of Garrett, 1980; the solid lines show linear approximations (NRC, 1981).

in how those concepts were applied to practical situations and in the methodology used to estimate RE. Currently, all systems use ME (or digestible proximate constituents) as the beginning point for estimation of feed value. The CNES lists NE_m and NE_g values for each feedstuff. Some have been measured, but most have been calculated from ME. All systems have adjustments in feed values for plane of nutrition or feed level. The adjustments were by constants or equations in some systems but inherent in others. For example, the CNES measures NE_g as the slope of the regression of RE on dry matter intake, with at least 2 levels of intake. Thus, correction for level of intake is imbedded in the NE_g estimate. The ARC system, in contrast, employed the use of an equation to adjust ME values for different levels of intake. All systems use a measured or estimated FHP as the basis for estimating NE requirements for maintenance. Metabolizable energy required for maintenance is defined as the MEI at which $RE = 0$ or $HE = MEI$. The NE required for maintenance is defined as FHP, which equates to NE_m . Estimates of efficiency of energy use for maintenance are estimated as FHP/ME required for maintenance or as the slope of the regression of RE on MEI when $RE \leq 0$. All systems use RE as NE for a productive function.

Systems differ in how basic NE concepts were applied and in methodology used to estimate HE or RE.

The CNES system was based exclusively on long-term, comparative slaughter studies. The ARC and other European systems were based primarily on short-term calorimetry experiments. Lower estimates of efficiency generally result from comparative slaughter trials as compared with calorimetric studies. These discrepancies may, in part, result from greater environmental effects and animal activity, as well as other energy losses not accounted for in short-term calorimetry studies (e.g., hair loss). Another difficulty for all systems is how to convert BW change to empty BW and body energy change and vice versa. Accurate prediction of feed intake often limits application of all systems to predicting animal performance in practical animal production.

As noted above, the CNES was originally developed as a system to express the energy values of feeds and stating energy requirements of growing beef cattle. The system was tested extensively at the California Experiment Stations and in commercial feedlots. It was readily accepted by nutritional consultants in the feeding industry. It was useful for evaluation of performance of growing cattle and was adopted by the NRC (1976).

At the time of development, British or crosses of British breeds (primarily Angus and Hereford) of cattle constituted the majority of the US cattle population. Those types of cattle were thus the primary re-

sources used to develop the CNES. In addition, those cattle were generally given a growth stimulant and fed in a thermoneutral environment. The original CNES did not accommodate cattle differing substantially in mature size, growth rate, or, as a result, differences in body composition and composition of BW gain at a given BW and rate of gain. This limitation increased in importance due to importation of a large number of different breeds of cattle and intensive selection for increased growth rate, mature size, and decreased body fat beginning in the late 1960s. Because the system was developed using cattle given growth stimulants (primarily diethyl stilbestrol), it was not directly applicable to cattle not given growth stimulants nor to those given different growth stimulants that resulted in altered body composition or rate and composition of BW gain. Likewise, the system was not readily amendable for use in adverse environmental conditions, nor did it account for differences due to age, previous growth rate, or feed intake.

The basic concepts incorporated into the sixth revised edition of Nutrient Requirements of Beef Cattle (NRC, 1984) were those described by the CNES (Lofgreen and Garrett, 1968) for feedlot cattle. However, the equations incorporated into the NRC (1984) recommendations were primarily based on those reported by Garrett (1980) and were developed from a much larger database than included in the original description of the CNES. Empirical equations (based on data from 1,049 cattle) to predict dietary NE_m and NE_g values from dietary ME content were included. Maintenance ($Mcal \times kg^{-0.75} \times d^{-1}$) for steers, heifers, bulls, and cows was estimated as $NE_m = 0.077W^{0.75}$. Discussion included the potential need to adjust maintenance requirements to reflect differences due to sex, breed, physiological state, and environmental conditions, but adjustments were not formally included in the system. Equations from Garrett (1980) to predict RE, hence animal NE_g requirements for feedlot cattle from BW and rate of gain, were included. Work of Fox and Black (1984), among others, provided impetus to incorporate adjustments to the system to address factors known to affect energy utilization and requirements. Adjustments to the basic equations to predict energy content of BW gain for large-frame size, compensatory gain (i.e., yearling- vs. calf-fed), sex, and for application to nonimplanted animals were included. The application of NE concepts to mature cows was expanded. The NE_g of mature thin cows was estimated to be 6.5 Mcal/kg of gain, and estimates of NE required for pregnancy and milk production, expressed as NE_m , were included.

A net carbohydrate and protein system for evaluating cattle diets (the Cornell Net Carbohydrate and Protein System; CNCPS) for predicting nutrient requirements, feed intake, and feed utilization of cattle was reported in detail by Fox et al. (1992), Russell et al. (1992), and Sniffen et al. (1992). The CNCPS broke from traditional NE systems that used MEI as the beginning point. The CNCPS included a model of rumen

fermentation that predicted rates of feedstuff degradation in the rumen, passage of undegraded feed to the lower gut, and the amount of TDN and protein available to the animal. To achieve these results, structural carbohydrate and nonstructural carbohydrate were estimated from sequential detergent analyses of the feed, and fractional rates of degradation of structural and nonstructural carbohydrate degradation were predicted. Crude protein was partitioned into 5 fractions and rates of degradation of each were estimated. Ruminal passage rates were calculated as functions of intake, particle size, bulk density, and type of feed. Total carbohydrate or crude protein digested in the rumen was calculated by use of the relative rates of degradation and passage. Fecal losses were calculated, and from those values, TDN was determined. Dietary ME was calculated from TDN. Subsequently, NE_m and NE_g were calculated from ME by use of the NRC (1984) equations. The CNCPS used equations of NRC (1987) to predict dry matter intake of growing cattle and beef cows.

The CNCPS defined the NE required for maintenance (Mcal/d) as:

$$NE_m = 0.077W^{0.75}$$

(Garrett, 1980) with empirical adjustments for acclimatization, breed, lactation, grazing (activity), and current effective environmental conditions (as affected by body condition, hair coat, temperature, wind, mud, moisture), which could result in cold or heat stress.

Requirements for growth were similar to NRC (1984), except adjustment factors for frame size 1 to 9 for bulls, steers, and heifers were included. Frame size was adjusted 1 size smaller for no implant and 1 size larger for an estrogenic and trenbolone acetate combination.

It is significant that the CNCPS extended the concepts of feeding systems to include prediction of nutrient requirements and described management for the entire life cycle of beef cattle well beyond what had been included in other systems in North America. The CNCPS incorporated more detailed and elaborate approaches for the estimation of requirements for optimum growth of replacement heifers and young cows than had been described previously. The CNCPS also incorporated a system of equations to describe breed, age, and stage of lactation effects on milk production level and energy required for milk production. The system also included a series of equations allowing prediction of energy requirements for pregnancy. The CNCPS incorporated approaches to assess body size and condition scores on energy reserves and how those estimates could be used to manage energy balance in cows.

The Nutrient Requirements of Beef Cattle, 7th revised edition (NRC, 1996), and the subsequent update (NRC, 2000) like the CNCPS, was anchored in the CNES. Many of the concepts incorporated into the recommendations (NRC, 2000) were similar to those of the CNCPS. The NE_m (Mcal/d) was defined as:

$$NE_m = 0.077EBW^{0.75}$$

(Garrett, 1980). Empirical adjustment factors for breed, sex, age, season, temperature, acclimatization, cold and heat stress, physiological state, activity, and previous nutrition or compensatory gain were included to address several factors known to affect maintenance requirements. Composition of BW change was estimated, and efficiency of body tissue loss for maintenance was estimated as 80%. As with previous NE systems, NE_g was defined as RE and equations were taken from NRC (1984) to convert RE to empty BW and empty BW gain and to shrunk BW and shrunk BW gain. The system developed for predicting energy and protein requirements of growing cattle assumed that cattle have a similar body composition at the same degree of maturity. Based on that premise, an equivalent BW concept was implemented by adjusting the BW of cattle of various body sizes and sexes to a BW at which they were equivalent in body composition to the steers in the Garrett (1980) database in which

$$EQSBW = SBW \times (SRW/FSBW),$$

where EQSBW = the weight equivalent to the NRC (1984) medium frame size steer; SBW = shrunk BW being evaluated; SRW = standard reference weight for the expected final body fat; and FSBW = final shrunk BW at the expected final body fat. Inclusion of this concept allowed incorporation of various factors such as compensatory gain, ionophore, anabolic agents, or breed effects that are expected to affect mature BW or slaughter weight as continuous rather than discrete effects.

As with the CNCPS, numerous additions were included in the NRC (2000) to allow application of NE concepts to express nutrient requirements during the life cycle of beef cattle. Examples include energy and protein requirements for breeding herd replacements, which included management recommendations to achieve target BW and rates of gain for replacement heifers and young cows. Estimation of energy and protein reserves of mature beef cows, their relationships with body size and cow BCS, and NE_m provided from body reserves or required to replace body reserves were included. In addition, nutrient requirements for reproduction and lactation were included.

In concept, the systems of expressing energy requirements of animals and values of feed resources to meet those requirements have not changed a great deal for many years. Primary changes have been to expand earlier systems to encompass more distinguishable segments of beef cattle production and include predictions relating to differing physiological states. Many of the modifications of these systems have been made in recognition that animal requirements are not static but are dynamic and vary in response to changing environmental conditions, change as animals undergo normal growth and development or undergo changes in physi-

ological state, or to represent animals of diverse genotypes. As a result, constants have become variables, in many cases, by simplistic empirical adjustments. Unfortunately, although those adjustment factors were applicable under the conditions of measurement, or were generally applicable, they may not be applicable to conditions outside the original conditions and are not likely to be additive as often assumed.

Representation of Biology—Models

Routine use of the energy systems for predicting animal performance for livestock feeding management is changing. Static systems of feed requirements are beginning to be replaced by dynamic simulation models able to characterize animal responses to a wider range of input conditions than previously possible. Dynamic models allow both inputs and outputs to vary within the period of interest, permitting characterization of an expanding set of management options such as limit feeding, sorting into uniform groups, and the use of new growth adjuvants like the β -adrenergic agents or recombinant bovine ST as well as consideration of individual animal differences and variable maintenance requirements. Further, transition states, not handled by static systems, may be simulated. Also, feed intake must be simulated. Our objective is to illustrate the contributions of specific models in better predicting animal performance and formulating rations. These models are mechanistic and based on the hypothesis that specific description of the governing biology coupled with proper application of mathematical modeling tools will result in greater accuracy and wider application than is usual with the older traditionally defined empirical approaches (feeding systems). Thus, the emphasis will be on biological relationships of nutrients and performance with their response surfaces and associated management or economic consequences, and not on set levels of requirements or tables.

Although adjustment factors are adequate in well-defined conditions, new situations with sets of input variables different than those for which the original adjustments were made may make predictions made using the factors erroneous. This is due to interrelationships between variables and thus a lack of independence among adjustment factors. Level 2 in the beef NRC (2000) attempted to address these issues. For example, to account for different types of rations, a different multiplier for the feed NE value may be needed for the effects of previous rate of gain. Thus, parameters within the model are not independent. Identification of unique values for the parameters leads to models that should be more robust when extended to new situations. Oltjen et al. (1986b) proposed use of a more general model of beef cattle growth and composition. Because cattle feeding programs range from low-quality forages to high-energy feedlot diets including multiphase systems in which several rations of widely varying energy content are fed, accurate prediction of

composition of gain is necessary for proper evaluation of animal value throughout the growing period. That is, market price is related to body composition, either as a discount for fat animals at preslaughter weight or at maximum for an optimum fat content for slaughter-weight animals. Oltjen et al. (1986b) developed a dynamic model (Davis growth model, **DGM**) based on general cell number and size mechanisms of growth to predict net protein synthesis and integrated the model into the Lofgreen and Garrett (1968) system described above to estimate gain of fat and lean tissue.

Three apparent determinants of growth in mammalian systems (Baldwin and Black, 1978) are used in the model: 1) the primary genetic determinant of organ size is the final DNA content of the organ in mature, normally grown individuals of the species and nutritional status determines the rate of DNA accumulation and whether target DNA content is achieved; 2) each unit of DNA specifies on a genetically defined basis for each tissue and each species, the ultimate formation of a specific amount of cell material, and nutritional and physiological status determines whether this target is achieved; and 3) the specific activities of enzymes responsible for tissue growth vary exponentially with organ size, and the kinetic properties of these enzymes are relatively constant across species. These concepts were discussed by Bywater et al. (1988) and were shown to describe growth of tissues and organs of rats, mice, sheep, and pigs (Baldwin and Black, 1978).

The same concepts and equation forms of Baldwin and Black (1978) served as the beginning point for the DGM. They initially developed a model of whole-body protein for normal, uninterrupted growth (Oltjen et al., 1985) using rats, because serial data on whole-body DNA were not available for cattle. The model was dynamic, thus differential equations were integrated to estimate gain (or loss) of DNA and body protein (**PROT**). Parameters were estimated using nonlinear least squares fit of observed body protein gains in 53 groups of feedlot steers (Oltjen et al., 1986b). For animals of different mature size, rate constants are adjusted by the size scaling factor proposed by Taylor (1980). Next, a data set (Garrett, 1980; W. N. Garrett, University of California, Davis, personal communication) containing initial and final empty BW and compositions and MEI for over 1,000 growing beef cattle were added to account for effects of energy intake on growth. A ratio, P , was defined as $MEI/MEINORM$, where $MEINORM$ (Mcal/d) = the pattern of MEI intake that supports normal growth of a reference steer (Oltjen et al., 1986b). Finally, daily empty body fat gain was calculated as the NE available after daily feed intake (kg/d) used for maintenance and protein gain was subtracted. Empty BW was the sum of fat and fat-free body mass, where fat-free body mass was $PROT/0.2201$ (Garrett and Hinman, 1969). Because the model requires initial estimation of whole-body DNA, protein, and fat, empirical relationships between these and ani-

mal BW, mature size, and condition score were used to set beginning values for model implementation.

The model was evaluated first with respect to its ability to predict growth and composition of steers as affected by nutrition, initial condition, frame size, and use of growth-promotants. Using 2 independent data sets, the model predicted empty BW and fat content with standard deviations of predicted minus observed of 14 and 10 kg, respectively (Oltjen et al., 1986b). No systematic biases were evident with respect to composition, frame size, or energy intake. However, fat gain was underpredicted ($P < 0.01$) at high feed energy concentrations. No adjustment for variable maintenance requirements could be identified. Baldwin and Bywater (1984) have shown other factors that affect energy expenditures are normally accounted for within the definition of maintenance. When dynamic properties and stability of the model were investigated (Oltjen et al., 1986a), prediction intervals (integration step size) of up to 7 d resulted in little increase in error if the coefficient of variation of feed intake was less than 15%. If the interval was 1 d, intake coefficient of variation could be as high as 40% with no loss of fit.

Although the DGM accounted for variations attributable to initial body composition and mature size, the model did not always yield acceptable estimates of fat gain. This was not unexpected, because fat accretion was computed after energy requirements for maintenance and protein gain were satisfied. Thus, any errors in estimates of maintenance or protein gain resulted in biased fat gain predictions. Further, feed energy available for fat accretion is not used at the same net efficiency as for energy gain of protein, as the NE system assumes (Berschauer et al., 1980). For example, of the major metabolites used for fat synthesis, fatty acids are the most efficient precursor, followed by glucose and propionate, with acetate being least efficient (Baldwin and Smith, 1979). Thus, for diets of similar NE_g , the one resulting in absorption of more fatty acids will support faster gains when the composition of gain is relatively greater in fat.

In recent years, attempts have been made to correct these nutrient partitioning and other errors, and integrated models of growth with digestion or metabolism, or both, have been developed. France et al. (1987) proposed a dynamic model of cattle growth based on carbon and N metabolism. State variables (quantities) were body protein, lipid and ash, and blood acetyl coenzyme A equivalents, blood glucose equivalents and blood amino acids. Inputs of rumen volatile fatty acids were converted stoichiometrically to their equivalent 2- or 6-carbon metabolites. Synthesis and degradation were represented for each body pool based on animal factors and absorbed nutrient levels. Compared with experimental data, relatively good agreement was observed, although information is limited where both absorbed nutrient profiles and body composition were simultaneously measured. France et al. (1987) sug-

gested linking the model with a simple model of rumen digestion (France et al., 1982) to complete the growth prediction system.

In a more complex model, Di Marco et al. (1989) extended the growth equations used in the DGM to 2 pools of protein (body and viscera), 2 associated DNA pools, and a body fat pool. Growth was represented as the difference between synthesis and breakdown of each protein and fat pool. Parameters for DNA accretion in each protein pool were estimated using data from a reference steer for which DNA was measured (Di Marco et al., 1987). Protein synthesis and degradation for body and viscera were similarly estimated from the reference steer, but in addition, synthesis depended on blood amino acid concentration, and degradation depended on catabolic hormone level. Lipogenesis was represented by Michaelis-Menton equations, which depended on anabolic hormones, plasma glucose, plasma acetate or fatty acids, and fat content. Lipolysis was similarly represented and depended on catabolic hormones, plasma fatty acids, and fat content. Empty BW was the sum of the protein and fat pools plus the water and ash associated with the protein pool (PROT weight/0.243).

Next, Di Marco and Baldwin (1989) integrated their growth model with digestion and metabolism elements. The integrated model (complicated and we direct the reader to the original reference) represents digestion as 6 nutrient fluxes, which were input to a metabolism component of 9 state variables. Five of the state variables were from the growth model (body and viscera DNA and protein and fat); the other 4 were used in the growth model as inputs (plasma amino acids, acetate, lipids, and glucose). Energy balance was achieved by adenosine triphosphate transactions including oxidation, expenditure, and nutrient turnover. The authors suggested that the model was useful for studies of complex interactions among diet, feed intake, age, physiological status, body composition, nutrient partitioning, and energy costs associated with maintenance and growth. In particular, partial efficiencies of absorbed nutrient use for different maintenance and production functions may be evaluated. Additional terms can be added to the protein and DNA synthesis equations to directly account for ST (Verde and Trenkle, 1987), estrogen, and β -adrenergic agent (Beermann et al., 1987) effects on cell proliferation and protein turnover, demonstrating the direct usefulness of the mechanistic approach of this model. In a parallel model of sheep growth, Sainz and Wolff (1990a,b) evaluated the probable direct effects on mechanisms of protein degradation and lipolysis by these agents. Research and further model development is warranted for determination of effects of nutrition on growth hormone, IGF, and their interactions (Anderson et al., 1988; Houseknecht et al., 1988; Elsasser et al., 1989). Perhaps adipose mass should also be represented by cell number and size, as well as location, if marbling is to be predicted (Cianzio et al., 1985).

Separation of the protein pools by Di Marco et al. (1989) may account for variable maintenance requirements demonstrated by Koong et al. (1982) wherein relatively smaller viscera was associated with decreased FHP. Also, the metabolism submodel should correct errors in prediction of fat gain, because the efficiency of the use of each nutrient is explicitly represented. In this regard, Sainz and Wolff (1990b) showed the importance of protein metabolism and its manipulation for lean growth as opposed to relatively smaller effects possible by manipulation of lipolysis for sheep. Nutrient prioritization, as in previous models, is not necessary, because equations representing affinity and use of metabolites allow direct competition for their use. Hence, when tested and accepted, this and similar models will also account for effects of previous plane of nutrition and interactions between level of feeding and ration energy concentration. Further, the explicit representation of digestion products suggests that feeds must be represented by their chemical constituents in future systems. At present, the complexity and lack of identity (additional experimental data are needed to set parameter values with confidence) preclude general use of these models (France et al., 1987; Fox et al., 1988; Di Marco et al., 1989).

However, the CNCPS, like Di Marco and Baldwin (1989), has a kinetic submodel of rumen fermentation and predicts rates of feedstuff degradation in the rumen, the passage of undegraded feed to the lower gut, and the amount of ME and protein that is available to the animal (Fox et al., 1992; Russell et al., 1992; Sniffen et al., 1992). In the CNCPS, structural carbohydrate and nonstructural carbohydrate are estimated from sequential detergent analyses of the feed. Data from the literature are used to predict fractional rates of structural carbohydrate and nonstructural carbohydrate degradation. Crude protein is partitioned into 5 fractions. The amount of carbohydrate or N that is digested in the rumen is determined by the relative rates of degradation and passage. Rumen passage rates are a function of intake, particle size, bulk density, and type of feed consumed. The ME is calculated from TDN, which is estimated by subtracting fecal losses (predicted) from dietary intake of protein, carbohydrate, and fat. No attempt is made to account for different metabolites absorbed, except to use the NRC (1984) equations to calculate NE_m and NE_g from ME concentration. Maintenance energy requirement depends on weight, level of production, activity, and environment (Fox et al., 1988). Growth requirements are similar to NRC (1984), with frame size (1 to 9) adjusted 1 size smaller for no implant and 1 size larger for an estrogenic and trenbolone acetate combination.

In the past decade, the Cornell group has developed the Cornell Value Discovery System to assist in decisions for individual growing cattle management (Guiroy et al., 2001; Fox et al., 2004; Tedeschi et al., 2004). The Cornell Value Discovery System software provides the following: 1) predicted daily gain, incremental cost of

gain, and days to finish to optimize profits and marketing decisions while marketing within the window of acceptable carcass weights and composition; 2) predicted carcass composition during growth to avoid discounts for under- or overweight carcasses and excess backfat; and 3) allocates feed fed to pens to individual animals for the purpose of sorting of individuals into pens by days to reach target body composition and maximum individual profitability. This allows mixed ownership of individuals in pens, determination of individual animal cost of gain for the purposes of billing feed and predicting incremental cost of gain, and providing information that can be used to select for feed efficiency and profitability. These outputs are based on the CNCPS with appropriate extension and modifications as detailed by the Cornell researchers in the 3 publications cited above; the use of NE remains the same.

In a more mechanistic approach to account for variable maintenance energy requirements, a collaborative effort between scientists in New Zealand, Australia, and the United States developed a dynamic model of the visceral protein (**v**), muscle protein (**m**), and fat (**f**) pools of a growing sheep (Soboleva et al., 1999). In the model, muscle and viscera each have an upper bound (m^* and v^* , respectively). For muscle, m^* is genetically fixed, although the possibility of reaching this level depends on both the current intake (MEI) and nutritional history of the animal. However, v^* is also affected by energy intake and depends on previous nutrition. As in the DGM, NE intake above maintenance (NE_g) is used for visceral and muscle tissue gain before its use for fat accretion. Net energy for gain drives the growth of muscle and viscera. Heat production for maintenance depends on MEI and changes asymptotically to new levels when MEI changes resulting in a lag in change of maintenance requirements after intake changes. Additional information regarding kinetics of the growth model is given by Oltjen et al. (2000). The heat production parameters for growing lambs (Ferrell et al., 1986) were fit dynamically, and HE per unit of protein mass of viscera is about 10 times that of muscle. Also, viscera respond faster than muscle to changing energy intake by the animal, but this change has some time lag. Therefore, maintenance requirement becomes a dynamic variable depending on nutritional history as well as current energy intake. Thus, the static form of maintenance function used in traditional feeding systems is probably inappropriate, especially for dynamic situations. One of the advantages of the way the model is formulated is that the performance of different functions describing animal heat production can be investigated. That is, the fit of the model to data, using either traditional NE concepts and maintenance energy (HP_{maint}), or more general functions for HP, can be compared with choose the best functional description.

We have recently refined this prediction system for ruminant animal growth and composition. Again, using sheep data sets from Nebraska (Ferrell et al., 1986)

and New South Wales (unpublished data), we have simplified the adjustments in the model for gain of muscle protein and loss of **f** at near maintenance feeding and, more precisely, estimated variable maintenance parameters. Previously, HP_{maint} was similar to the Australian feeding system (AAC, 1990) based on Corbett et al. (1987) but with a variable coefficient on BW:

$$HP_{\text{maint}} = \alpha_t \text{EBW}^{0.75} + 0.09 \text{MEI}$$

$$\alpha_t = \alpha_0 [1 + b (\text{MEI}_t/\text{MEI}_0 - 1)(1 - e^{-t/\tau})],$$

which results in a lag in change of maintenance requirements after intake changes from MEI_0 to MEI_t . Here EBW = empty BW; t = time (d), b and τ = constants; and MEI_0 and α_0 = original values of intake and the maintenance coefficient, respectively. Fit of the Nebraska data (Ferrell et al., 1986) shows that the double correction for variable maintenance is not necessary; the previously used coefficient on MEI, 0.09, is not different than zero. Thus:

$$HP_{\text{maint}} = \alpha_t \text{EBW}^{0.75}$$

with improved estimates for b (0.116) and τ (20.0 d) (Figure 4). Alternatively, with the new equation for viscera, the multiple regression prediction of heat production using m , v , and their accretion (Oltjen and Sainz, 2001) is also improved (data not shown).

Overall, these changes significantly improve the prediction of body fatness as a function of BW and gain. Sheep growth and composition is more accurately predicted with the revised model, and the model predicts EBW and **f** content more accurately (± 2.1 kg and 2.3% units, respectively; Ferrell et al., 1986) than the current feeding system (AAC, 1990). New additions refine predictions at levels of energy intake at or below maintenance. The model provides the structure for predicting composition of growing cattle as well, but not all its parameters have been estimated and evaluated.

Barioni et al. (2006) added the variable maintenance representation from the sheep model to the DGM for beef cattle. Fitting beef cattle growth data, variable instead of fixed maintenance requirements for each experimental group significantly improved the precision of the model for **f** and RE, confirming the conclusions of Sainz et al. (1995) that previous nutrition had substantial effects on maintenance energy expenditures and indicates that variable maintenance can significantly improve model predictions. Sainz and Bentley (1997) showed that the observed changes in maintenance energy expenditures were closely related to changes in visceral protein mass.

Garcia et al. (2007) compared the DGM with a dynamic French model (**IGM**) also developed to predict protein and fat deposition in growing cattle (Hoch and Agabriel, 2004). Both models gave accurate and pre-

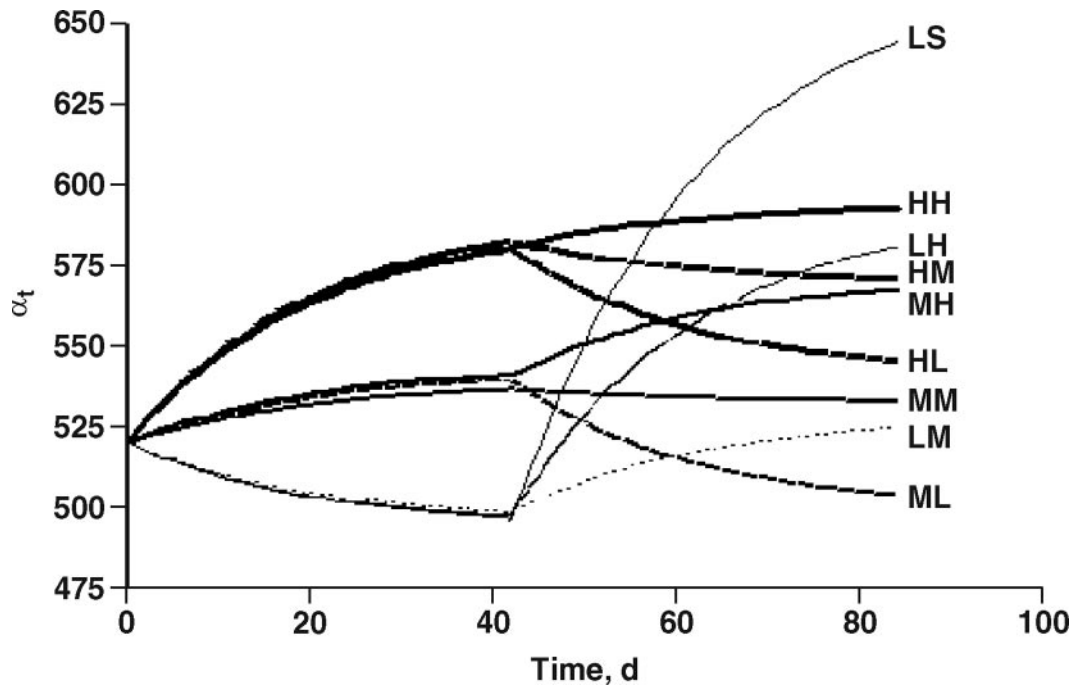


Figure 4. Model predicted maintenance coefficient (α) as a function of time (t) for the 9 treatment groups of Ferrell et al. (1986). Forty-eight intact male lambs (30 kg of BW) were fed to gain 16 (H), 5 (M), or -6 (L) kg during a 42-d interval (period 1). Lambs from each of the H and M groups were fed to gain 16 (HH, MH), 5 (HM, MM), or -6 (HL, ML) kg, and lambs from the L group were fed to gain 27 (LS), 16 (LH), or 5 (LM) kg during the ensuing 42 d (period 2).

cise predictions of body protein. They also performed well for prediction of body fat in continuously growing animals. However, DGM tended to underestimate body fat deposition during feed restriction periods. This suggests that DGM overestimated heat production during periods of low MEI. The IGM was not sensitive enough to MEI, because it overestimates body fat at low MEI and it underestimates body fat at high MEI. Also, IGM does not take into account ME concentration of the diet and thus did not simulate different growth trajectories for same MEI but different ME concentrations. These results suggest that model's structure and equations for protein accretion in DGM and IGM are valid. Future improvements will focus on prediction of heat production during feed restriction periods for DGM, confirming the need for a variable maintenance component, and on mathematical formulation of feed energy utilization for fat synthesis for IGM to improve model sensitivity to MEI.

Most recently, McPhee et al. (2007a,b) has extended the DGM to 4 fat depots: intermuscular, intramuscular, subcutaneous, and visceral, again based on DNA and cell size concepts. Fat depot parameters were estimated, and no differences between implant status and frame size were detected. The model currently underpredicts f in all 4 f depots for finishing steers fed high-concentrate diets, which suggests that a secondary phase of hyperplasia may be occurring, which is not represented in the DGM.

Conclusions

Several statements may be made that summarize the progression of models of energy use for beef cattle growth. Generally with each new system, the advance in prediction accuracy came about by adding new terms to conceptually validated models that were already accepted and in use. These terms were added using mechanistic concepts (France and Thornley, 1984) and representations of biological functions at lower levels of aggregation. Thus, it was the emphasis on the biology of processes involved, and not just another empirical fit or relationship, that extended the accuracy and precision with each new model. This evolutionary process will continue, adapting new research knowledge so that beef cattle growth and performance may be better predicted. The challenge is to deliver these newer systems, which necessarily require many calculations and hence computers for implementation. Additional inputs needed for the more complex models may require expert systems to assist the user to gain the additional information available from these systems with ever-increasing ranges of applications. The advantage then is their generality and ability to be integrated with other models allowing economic evaluation. This will eventually allow users to automatically search for solutions that approach optimal production strategies.

Recommendations. For future beef energy systems and research to assist in their preparation, the

following are proposed. 1) Evolution of models should continue, and they should be adopted in future feeding systems. 2) Experiments should be conducted so that dynamic model parameters and their distributions may be estimated. These include not only those directly related to digestion and metabolism but also those related to animal genotype. A particular area of concern is that EPD, both within and across breeds, or genetic markers, or both, be linked to model parameters. 3) Outputs should be tailored so that integrated management and economic evaluations are possible. 4) Inherent variation within animal and ration effects should be included and quantified. 5) Heuristic (expert systems and adaptive filtering) implementations of future systems should be accommodated, especially for inputs. 6) Environmental effects should be included in models mechanistically. 7) Protein-energy relationships should be included in metabolic submodels mechanistically. 8) Descriptions of feeds by chemical components and physical (digestion) characteristics should be initiated. 9) Observations and models should remain in the public domain where researchers can openly determine and correct deficiencies.

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